Genetic factors increasing male facial masculinity decrease facial attractiveness of female relatives

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Abstract

For women, choosing a facially masculine man as a mate is thought to confer genetic benefits to offspring. Crucial assumptions of the hypothesis have not been adequately tested. It has been assumed that variation in facial masculinity is due to genetic variation, and that genetic factors that increase male facial masculinity do not increase facial masculinity in female relatives. From facial photos, we objectively quantified facial masculinity of identical and (N=411) and nonidentical (N=782) twins and their siblings (N=106). Using biometrical modelling, we show that much of the variation in male and female facial masculinity is genetic. However, we also show that masculinity of male faces is unrelated to their attractiveness and that facially masculine males tend to have facially masculine, less-attractive sisters. These latter findings challenge the idea that facially masculine men provide net genetic benefits to offspring, and call into question this popular theoretical framework.

Introduction

A large body of research has shown that women attend to facial masculinity when assessing potential mates. Women tend to show greater preference for facially masculine mates in circumstances thought to increase the relative importance of indirect benefits of mate choice (i.e. genetic benefits to offspring) as opposed to direct benefits of mate choice (e.g. resource provision, protection). For example, women show greater preference for facially masculine men when considering a short-term or extra-pair partner (Little, Jones, Penton-Voak, Burt, & Perrett, 2002), during the fertile phase of the menstrual cycle (Gangestad, Thornhill, & Garver-Apgar, 2010; Penton-Voak et al., 1999), when sex-drive is high (Welling, Jones, & DeBruine, 2008), when self-perceived attractiveness is high (Little, Burt, Penton-Voak, & Perrett, 2001), and when pathogens are prevalent or health is threatened (DeBruine, Jones, Crawford, Welling, & Little, 2010; Little, DeBruine, & Jones, 2011). These studies largely focus on masculine face shape, as opposed to other features such as shading or texture. The widely accepted interpretation of these findings is that male facial masculinity is a signal of genetic quality ('good genes') and that women have accordingly evolved to attend to facial masculinity when making mate choice decisions (Gangestad & Simpson, 2000; Little, Jones, & DeBruine, 2011; Roberts & Little, 2008).

Facial masculinity is thought to be an honest signal of genetic quality because of the immunosuppressive effects of testosterone (Folstad & Karter, 1992), the idea being that only men with good innate immune functioning can afford to support the levels of testosterone required to develop masculine facial features (Folstad & Karter, 1992; Zahavi, 1975). Supporting this immunocompetence handicap hypothesis, facial masculinity is associated with circulating testosterone levels (Penton-Voak & Chen, 2004), and male facial masculinity has been found to correlate with both perceived and actual health (Rantala et al., 2012; Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006). An alternative (or additional) explanation of the relevance of male facial masculinity to genetic quality is the 'sexy-son hypothesis', in which the genetic benefits to offspring are in the form of greater attractiveness of male offspring. This situation can create a self-reinforcing ‘runaway’ effect, exaggerating both the preference and the preferred trait (Fisher, 1915; Huk & Winkel, 2008).

The idea that male facial masculinity signals heritable genetic quality, reflected as immunocompetence and/or sexy sons, has gained broad acceptance (Gangestad & Scheyd, 2005; Gangestad & Simpson, 2000; Little, Jones, et al., 2011; Perrett et al., 1998; Rantala et al., 2012; Roberts & Little, 2008, although see Puts, 2010; Scott, Clark, Boothroyd, & Penton-Voak, 2012) – however, it depends on two key assumptions that have not been adequately tested: first, it is assumed that male facial masculinity is substantially heritable (i.e. a substantial proportion of the variation is due to additive genetic variation) – otherwise, it could not be inherited by offspring and could not signal good genes. Second, it has been assumed that the genes that increase male facial masculinity are not detrimental to females (e.g. by increasing their facial masculinity, which has been previously shown to decrease female attractiveness) – otherwise, any genetic benefits to male offspring would be counteracted by the detriment to female offspring (this is termed intralocus sexual conflict, see (Bonduriansky & Chenoweth, 2009; Garver-Apgar, Eaton, Tybur, & Thompson, 2011).

Only one previous study has empirically addressed these assumptions (Cornwell & Perrett, 2008), by analysing ratings of masculinity and attractiveness ratings of the faces in family photographs. However, there were no objective masculinity measures, and heritability could not be estimated because members of a standard nuclear family equally share both genes and family environment, which are therefore completely confounded. Additionally, a study presently under review used facial photos of identical and nonidentical twins to distinguish the influence of genes and family environment on facial masculinity and attractiveness but, again, no objective measures were employed (Mitchem et al., In Press). It has previously been shown that subjective ratings of masculinity are based on additional factors other than morphological masculinity, changing the association with traits such as attractiveness (Scott, Pound, Stephen, Clark, & Penton-Voak, 2010).

Here we use geometric morphometrics, the statistical analysis of shape, to objectively quantify the masculinity of facial shape in photographs of a large sample of identical and nonidentical (same-sex and opposite-sex) twins and siblings. Using biometrical modelling we estimate the heritability of male and female facial masculinity. Finally, we test for intralocus sexual conflict by assessing the correlation in facial masculinity between opposite-sex twins/siblings, and we investigate the relationship in each sex between the objective masculinity and rated attractiveness of the photographs.

Method

Participants

Participants were 1193 twin individuals and 106 of their siblings from 575 families who took part in the Genes for Cognition study and part of the Brisbane Adolescent Twin Studies (Wright & Martin, 2004). Twins were tested (and photographs taken) as close as possible to their 16^{th} birthday (M = 16.03±.47 years) and their siblings as close as possible to their 18^{th} birthday (M = 17.80±.46). See Table 1 for more details on the sample.

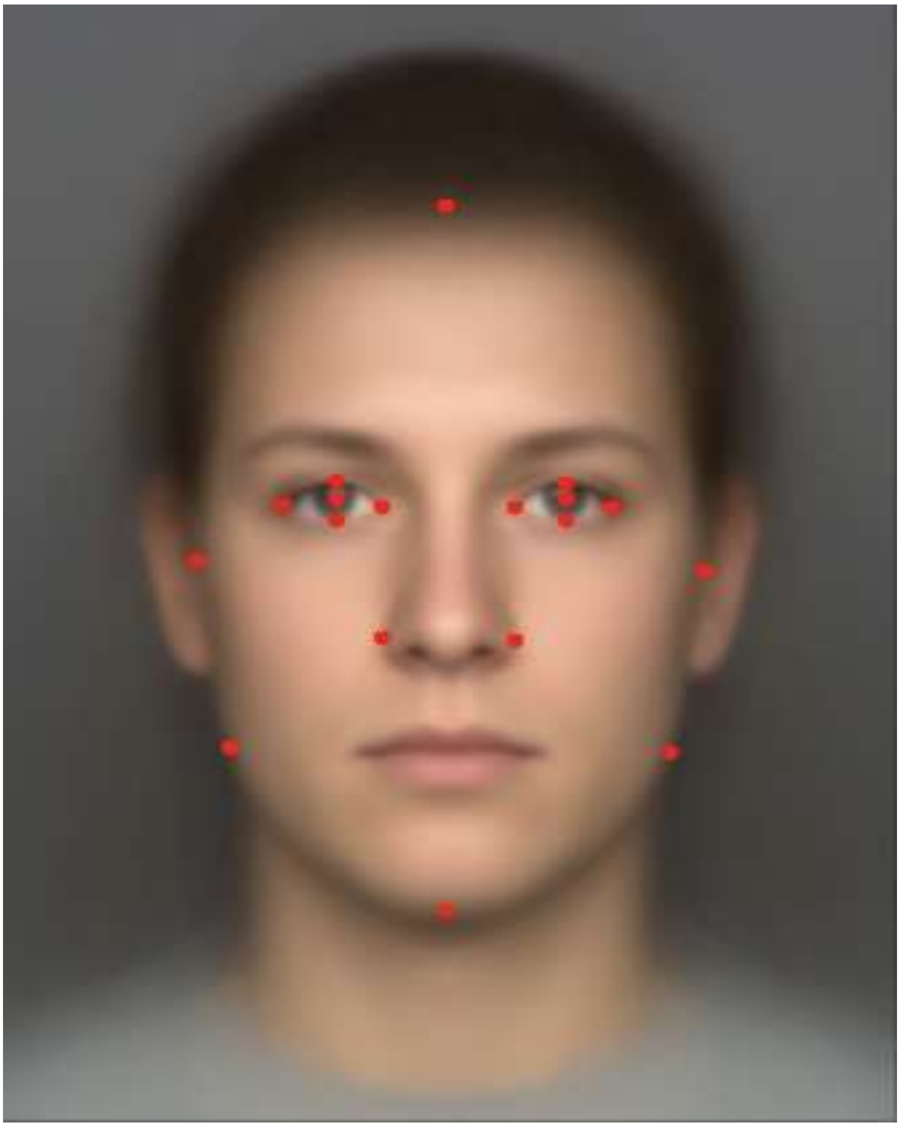

Figure 1. Facial landmarks used to compute facial masculinity.

Photographs

Photographs of participants were taken between the years of 1996 to 2010. In the earliest waves of data collection, photographs were taken using film cameras, and later scanned to digital format. Photographs from later waves were taken on digital cameras. Each photograph was taken under standard indoor lighting conditions. Objective masculinity and subjective ratings of masculinity and attractiveness were obtained from these photographs.

Ten independent raters identified a total of 18 landmarks on each face. Raters were trained for several weeks in hour-long sessions where landmarks were defined using anatomical definitions.

See Figure 1 for descriptions of each landmark. Two raters were randomly chosen for each landmark, and the coordinates were calculated as the mean pixel location from these two raters.

We note that photographs of participants were not originally taken for shape analysis. As such, variation existed between photographs that could alter the shape information captured by the landmarks (e.g., the participant's head angle facing the camera, or the participant's facial expression). We assume most of this type of variation is idiosyncratic between photographs and would therefore simply add error variance rather than biasing the results in any particular direction. However, to avoid the potential for smiling biasing the measures we did not use landmarks around the mouth, and we subsequently confirmed that controlling for rated degree of smiling did not affect the results (data not shown).

Facial Masculinity Scores

Geometric morphometrics was used to analyse the facial landmark coordinates. Geometric morphometrics is the statistical analysis of shape through landmark coordinates (Zelditch, Swiderski, Sheets, & Fink, 2004). Shape is defined as differences between objects that are not due to translation, size, or rotation, and therefore encapsulates all other information such as distances and angles between different landmarks.

In order to extract shape information from raw facial landmarks, a Generalised Procrustes Analysis (GPA; see Zelditch et al., 2004) was conducted on raw x- and y-coordinates. This procedure removes translation effects (position of the object in the shape space) by standardising to a common shape space, size effects by standardising centroid size to one, and rotational effects by minimising the summed squared distances between homologous landmarks between faces. This produces new coordinates (Procrustes coordinates) that purely represent shape information. The Procrustes coordinates were then transformed into shape variables via a Principal Components Analysis. Shape variables are a decomposition of the original Procrutes coordinates, and completely maintain the shape information. Shape variables also have the advantage of being compatible with conventional statistical techniques without the need for adjustments. For full details of GPA and shape analysis via geometric morphometrics, see (Zelditch et al., 2004).

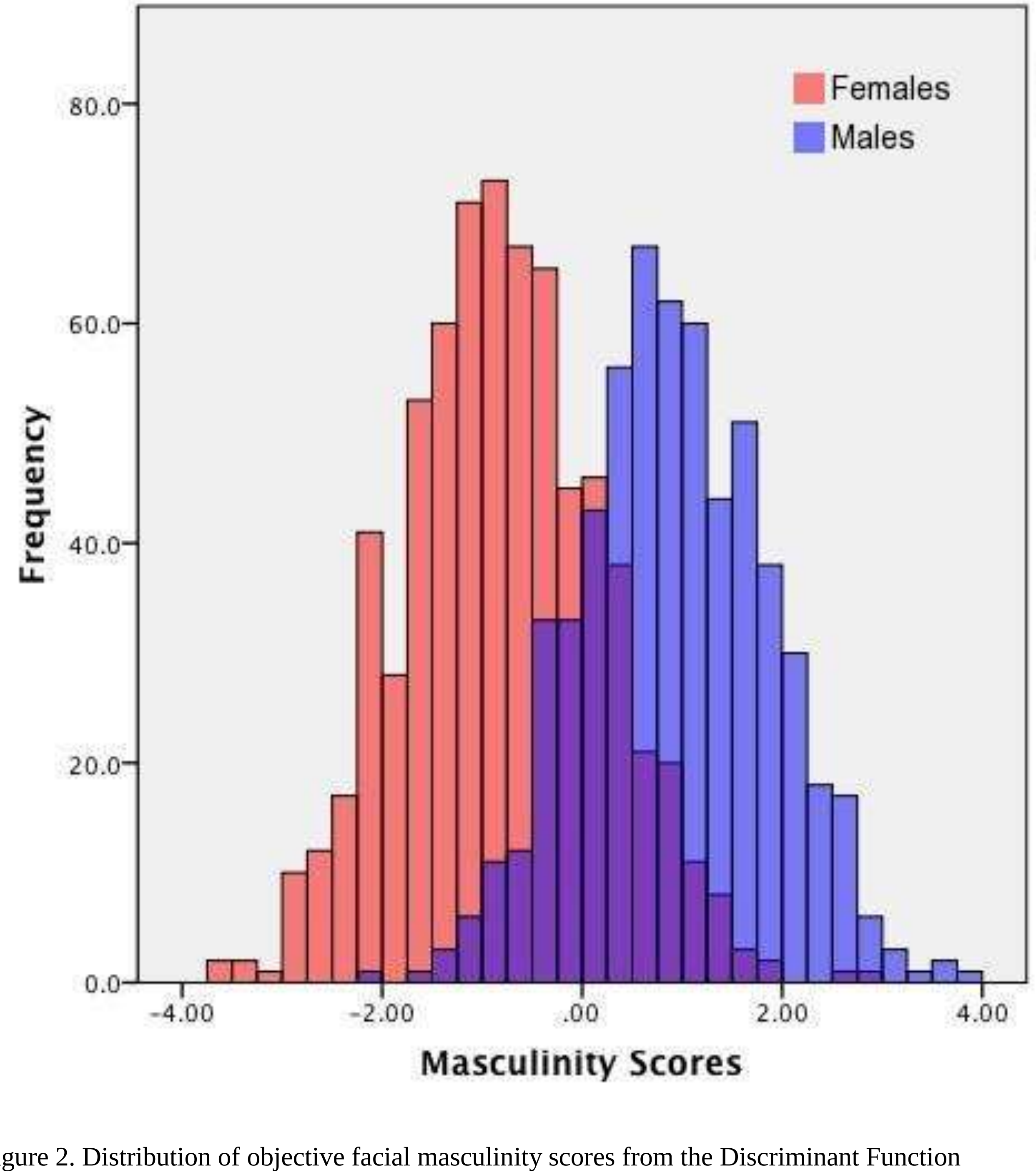

Figure 2. Distribution of objective facial masculinity scores from the Discriminant Function Analysis for men (M = .92 ± .94) and women (M = -.80 ± .97), before standardization separately by sex.

In order to compute a data-driven single measure of facial masculinity, a discriminant function analysis (DFA) was conducted with sex as the grouping variable (females = 0, males = 1). DFA produces a discriminant function, which is the linear combination of shape variables that best discriminates between male and female landmark configurations. As such, the discriminant function from this analysis represents the sexual dimorphism dimension (see Figure 2 for distribution of scores on the discriminant function). Related analyses have previously been used to compute data-driven scores of facial masculinity (Gangestad et al., 2010; Scott et al., 2010). The DFA was performed in the twins, yielding a point-biserial correlation of .66 between participant sex and the discriminant scores, slightly higher than the corresponding value reported in Gangestad et al., (2010). The discriminant function correctly classified the sex of 81% of participants – this is lower than the corresponding value reported in Scott et al. (2010), but their high ratio of predictors to participants (which can cause model-overfitting) and lack of cross-validation make it difficult to interpret their very high rate of correct-classification. To cross-validate our measure, we applied this same function to the siblings – this yielded a point-biserial correlation between sex and masculinity of .65 and a correct-classification rate of 80%, indicating that the masculinity measure discriminated between the sexes equally as well in the ~18 year old siblings as in the ~16 year old twins, further validating our measure. The discriminant scores were standardised by sex in order to produce a facial masculinity score for each individual in relation to others of their own sex. Five outliers on facial masculinity (± 3 *SD* from the mean) were omitted from all analyses, although note an analysis retaining these outliers yielded virtually identical results (data not shown).

Observer Ratings of Facial Attractiveness and Masculinity

Photographs were also rated by observers on a number of traits. For this paper, we are primarily interested in the attractiveness ratings, but also report on the facial masculinity ratings to check whether face shape masculinity scores calculated from landmark coordinates correlated with subjective perceptions of facial masculinity. Eight undergraduate research assistants (four males, four females; different individuals from those who identified the facial landmarks) were presented the photos in a random order and rated all faces on attractiveness and facial masculinity. Ratings were given on a 7-point scale (1 = low attractiveness, 7 = high attractiveness and 1 = very feminine, 7 = very masculine for attractiveness and masculinity respectively). Raters were not given instructions on how to judge attractiveness, though were informed of facial features that are considered to be sexually dimorphic in humans. Inter-rater agreement for attractiveness was moderate (intraclass correlation=.44, p<.001; α = .87). Separate composite (averaged) scores comprising raters of each sex correlated very highly with a composite score comprising all raters (r=.94 for male raters and r=.92 for females), so the combined composite score was used for all analyses since it contained substantially less measurement error. Inter-rater agreement was low for masculinity (ICC=.19; α = .66). Nevertheless, there was still a significant (though modest) correlation between objective and rated masculinity (r=.23, p<.001 in males, r=.25, p<.001 in females). Note also that objective masculinity was based only on shape, and was not associated with ratings of grooming or acne, whereas masculinity ratings were associated with ratings of grooming (females: r=-.44, p<.001; males: r=-.05, p=.29) and acne (females: r=.29, p<.001; males: r=.21, p<.001) and were presumably influenced by other cues such as skin colour and tone, heaviness of brow and face hair, etc., as well as shape. Consistent with this, our objective masculinity measure correlated much more strongly with the component of the masculinity ratings that is captured by the landmark-based shape variables ($r = .53$, $p < .001$ for males, $r = .57$, $p < .001$ for females) than with the raw masculinity measure – see online Supplemental Material for details of the analysis.

For more detail on the rating process and genetic analyses of observer ratings, see Mitchem et al., (In Press).

Statistical Analysis

Identical twins share all their genes whereas nonidentical twins share on average half of their segregating genes, and all twins completely share the family environment; as such, we were able to partition the variation in scores into three sources: additive genetic (A), shared environmental (C), and residual (E) sources. As is standard for twin-family designs, biometrical modelling was conducted using maximum likelihood modelling, which determines the combination of A, C, and E that best matches the observed data (i.e. means, variances, and twin/sibling pair correlations). For further detail of twin analysis, see (Neale & Cardon, 1992; Posthuma et al., 2003). All analyses were conducted in the Mx software package (Neale, Boker, Xie, & Maes, 2006). As is standard in twin modelling, differences between the means and correlations of different zygosity groups were tested by equating the relevant parameters in the model and testing the change in model fit (distributed as χ^2) against the change in degrees of freedom (which equals the change in the number of parameters estimated).

Results

Preliminary testing found that mean facial masculinity did not significantly differ between identical and nonidentical twins of the same sex (χ^2 (2) = 2.48, p = .29); importantly, means of female (or male) members of same-sex pairs did not differ significantly from female (or male) members of opposite-sex pairs (χ^2 (2) = .31, p = .85), suggesting no influence on this trait of any prenatal hormone-transfer from one twin to the other. Means of twins did not significantly differ from means of other siblings (χ^2 (2) = 3.60, p = .17) suggesting nothing unusual about the facial masculinity of twins. Furthermore, correlations between nonidentical twin pairs (male-male, female-female, and male-female) did not significantly differ from the correlations between corresponding non-twin sibling pairs (χ^2 (3) = 2.18, p = .54), as expected given equivalent genetic and environmental similarity of nonidentical twin and sibling pairs; these correlations were equated in subsequent modelling. There was no significant effect of age on facial masculinity in males (χ^2 (1) = .04, p = .85) or females (χ^2 (1) = .63, p = .43). Intraclass correlations are shown in Table 1. Correlations between identical twins were markedly greater than correlations between same-sex nonidentical twins/siblings for both males (χ^2 (1) = 11.92, p < .001) and females (χ^2 (1) = 4.93, p = .03), suggesting an important genetic component for facial masculinity in both sexes. The estimated proportions of variation in facial masculinity due to genetic and environmental sources are reported in Table 2. For both males and females, around half of the variation in facial masculinity was attributed to additive genetic factors, while virtually no variation was attributed to shared environmental influences. This is consistent with the assumption that variation in facial masculinity is substantially heritable, which is a necessary condition for facial masculinity to serve as a signal for good genes.

Table 1. Intraclass twin/sibling pair correlations (and 95% confidence intervals) for objective facial masculinity.

Zygosity	*r* (95% CI)
Identical female twins (N pairs = 110)	.50 (.36, .61)
Identical male twins (N pairs = 88)	.50 (.34, .62)
All identical twins	.50 (.39, .59)
Nonidentical female twins (N pairs = 113)	.30 (.11, .45)
Female siblings (N pairs=55)	.20 (-.16, .46)
All nonidentical female twins/siblings	.28 (.11, .42)
Nonidentical male twins (N pairs = 93)	.16 (-.04, .35)
Male siblings (N pairs=39)	-.09 (-.38, .22)
All nonidentical male twins/siblings	.09 (-.08, .26)
All nonidentical same-sex twins/siblings	.23 (.10, .35)
Nonidentical opposite-sex twins (N pairs = 171)	.23 (.09, .36)
Opposite-sex siblings (N pairs=120)	.23 (.04, .39)
Opposite-sex twins/siblings	.23 (.12, .33)

NB: Means and variances were equated across zygosity (within sex). Sibling pairs are not independent, e.g. one non-twin sibling can have a sibling relationship with each member of a twin pair.

Table 2. Proportions of variance (and 95% confidence intervals) of objective facial masculinity estimated to be accounted for by A (additive genetic), C (shared environmental), and E (residual) influences

	A	C	E
Female	.48 (.11, .61)	.03 (.00, .34)	.49 (.39, .62)
Male	.46 (.20, .59)	.00 (.00, .17)	.54 (.41, .71)
Overall	.49 (.28, .57)	.00 (.00, .17)	.51 (.43, .61)

NB: Opposite-sex twins contributed to means and variances, but not to variance components (i.e. genetic correlation between opposite-sex twins was left free to vary in the model). The genetic correlation between opposite-sex twins was estimated in the model at .50, the same as same-sex nonidentical twins, implying no sex-limitation in facial masculinity, i.e. a perfect genetic correlation (r_g=1.0) between male and female facial masculinity.

One of the main goals of our analysis was to determine the degree to which genes that affect masculinity in males have that same effect in females. The significant positive association of facial masculinity between opposite-sex twins and siblings (r=.23, p<.001, see Table 1) suggests that heritable factors that increase male facial masculinity also increase female facial masculinity. In fact, the opposite-sex twin/sibling pair correlation was of similar magnitude to that of the same-sex nonidentical twin/sibling pairs, suggesting that the same genes influence male and female facial masculinity (accordingly, modelling showed a genetic correlation between the sexes of 1.0 (p=.02), see footnote to Table 2). Masculine female faces were rated as less attractive than feminine female faces by observers (r=-.17, p<.001). This suggests that the heritable factors underlying male facial masculinity reduce female attractiveness. Accordingly, the correlation between brother masculinity and sister attractiveness was *r* =-.13 (p =.03); that is, sisters of more facially masculine men are less facially attractive. Therefore, any genetic benefits to male offspring associated with choosing a facially masculine partner would be countervailed by reduced attractiveness of female offspring. In contrast, and unsurprisingly, there was no association between sister facial masculinity and brother facial attractiveness (r=-.02, p=.72).

Furthermore, in contrast to females, male facial masculinity was not associated with rated attractiveness (r=.01, p=.84), calling into question the 'sexy sons' hypothesis whereby male facial masculinity is preferred for heritable attractiveness.

Discussion

Despite the large proportion of variation in facial masculinity that we estimated to be due to additive genetic influences (49%), our other findings do not support the widely held framework that male facial masculinity is a signal for heritable genetic benefits, for two reasons. First, there was no association between male facial masculinity and rated attractiveness, contrary to the 'sexy sons' explanation of facial sexual dimorphism. This is by far the largest sample that has been used to assess how natural variation in objective facial masculinity affects individuals' attractiveness, and the finding accords with the overall picture from previous experimental and correlational research showing mixed findings as to whether male facial masculinity is attractive, unattractive, or neutral (DeBruine, Jones, Smith, & Little, 2010; Perrett et al., 1998; Rhodes, 2006; Scott et al., 2012).

Second, we found that the same genetic factors increased male and female facial masculinity. Combined with the negative association of female facial masculinity and attractiveness, this suggests the genetic factors increasing male facial masculinity decrease facial attractiveness in female relatives. Accordingly, more facially masculine males had less facially attractive sisters. A sister shares the same proportion (50%) of segregating genes as a daughter, suggesting that choosing a facially masculine male as a mate will tend to decrease the attractiveness of resulting daughters. It is possible that yet-to-be-established genetic benefits to sons outweigh these genetic detriments to daughters – however, any such genetic benefits would need to outweigh not only the detriment of masculinity to female facial attractiveness as found here, but perhaps also apparent detriments to female fertility (Pfluger, Oberzaucher, Katina, Holzleitner, & Grammer, 2012) and health (Thornhill & Gangestad, 2006).

The existence of facial sexual dimorphism suggests there have been different selection pressures on male and female facial shape, and that masculine male faces have (had) a selective advantage of some kind. Our results are difficult to reconcile with the notion that the selective advantage of masculine male faces comes from female preference for facially masculine men for genetic benefits to offspring, but our results do not preclude this type of explanation. For example, it is possible that masculine faces, while not judged as being more attractive by raters overall, are judged as more attractive by females who are ovulating or in certain contexts or populations. Another alternative is that female choice does not act on facial masculinity per se, but on correlated traits such as body muscularity or assertive behavioural tendencies.

Moreover, the advantages of male facial masculinity may stem from enhanced fitness from factors that do not have to do with female choice. For example, facially masculine men might gain a survival or reproductive advantage through intrasexual competition by being more robust to physical damage or by signalling formidability and dominance to male competitors (Puts, 2010). In contrast to the findings for masculine male faces, female facial femininity (i.e. low masculinity) is heritable, is associated with attractiveness, and does not affect brother facial attractiveness, so a male choosing a feminine mate would increase the attractiveness of daughters with no detriment to sons' attractiveness (although there could be disadvantages in terms of body morphology or behavioural assertiveness – the corollary of the caveats mentioned above). Unlike masculine male faces, feminine female faces are robustly preferred across studies and have been shown to be even more strongly preferred after exposure to pathogen cues and by males with high levels of pathogen sensitivity (Lee et al., 2013; Little, DeBruine, et al., 2011), perhaps suggesting a pathogen-related advantage of feminine faces. All this warrants more research into male choice of facially feminine females and the possible direct or indirect (genetic) benefits to offspring.

A potential limitation of our study is that the facial photographs of twins were taken when they were 16-years-old, at which time facial masculinity might not have yet fully developed. However, the following observations suggest the findings would likely hold in an older sample: a) facial dimensions are more than 94% of their adult sizes by age 16 in both males and females (Edwards et al., 2007), b) there was no mean effect of age on the facial masculinity measure in the sample including older siblings, c) the facial masculinity measure derived from the 16-year-old twins discriminated the sexes equally as well in the 18-year-old siblings, and d) correlations between twins and older siblings showed the same pattern as within the twins. Other limitations include standard caveats of the classical twin design – in particular, we need to keep in mind the possibility that our biometrical modelling could have overestimated additive genetic effects and underestimated shared environmental and nonadditive genetic effects, because these two latter effects are negatively confounded when they are estimated using only twins (Keller & Coventry, 2005; Keller, Medland, & Duncan, 2010). Future research could overcome this issue by adding other members of twins' families, especially parents.

Assuming our results are generalizable, how might we explain the findings in light of aforementioned research showing greater preference for masculine faces in (for example) contexts of disease threat (DeBruine, Jones, Crawford, et al., 2010; Little, DeBruine, et al., 2011)? It has recently been suggested that male facial masculinity may signal direct benefits (Scott et al., 2012) rather than indirect (genetic) benefits. For example, partners that possess markers of good health due to immunocompetence may be preferred because they are less likely to succumb to disease, which would decrease their resource provisioning ability and increase the likelihood of transferring disease to the choosing individual or mutual offspring (Tybur & Gangestad, 2011). Other authors have suggested that male facial masculinity may be a signal for ability to compete intrasexually for resources or mates (Little, DeBruine, & Jones, 2012; Puts, 2010; Scott et al., 2012). How these various explanations might be distinguished has not been fully resolved (Gangestad & Eaton, 2013; Little, 2013), but the findings reported here call into question the predominant theoretical framework that explains preferences for male face shape masculinity in terms of genetic benefits for offspring.

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Ethical Statement

All participants gave informed written consent, and approval to code and analyze this data was obtained from the Human Research Ethics Committee at the Queensland Institute of Medical Research.

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